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Short Communication

Two decades of altered snow cover does not affect soil microbial ability to catabolize carbon compounds in an oceanic alpine heath

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ABSTRACT

Snow strongly affects ecosystem functioning in alpine environments with potential carry-over effects outside of snow periods. However, it is unclear whether changes in snow cover affect microbial community functioning in summer. In a field experiment, we tested whether manipulation of snow cover affected the functional capabilities of the microbial community either directly, or indirectly through concomitant changes in the vegetation. While 23 years of differential snow depth and persistence fundamentally changed the vegetation composition, the microbial community's ability to catabolize a range of carbon compounds was not altered. Instead, soil moisture content was the key driver of carbon catabolism by the microbial community.

In alpine environments snow cover is a major determinant of vegetation composition and biogeochemical cycling (Jusselme et al., 2016; Walker et al., 1999). Many mountain regions are experiencing reduced snow fall due to increasing temperatures and more precipitation falling as rain (IPCC, 2013). This results in shallow and intermittent snow covers, particularly in oceanic climates (McCabe and Wolock, 2010). Less snow leads to more frequent freeze-thaw events, which affects microbial community functioning (Matzner and Borken, 2008; Tierney et al., 2001) and alters vegetation composition (Scott et al., 2007; Welch and Scott, 2000). Plant species differ widely in rooting pattern and belowground productivity, as well as the quality of their litter and root exudates, all of which are known to affect microbial community composition (Bardgett et al., 2014). Winter snow regime is known to affect growing season microbial community composition (Wipf and Rixen, 2010; Zinger et al., 2009, but see Björk et al., 2008). However, whether snow regime also impacts summer microbial functioning, such as their ability to process carbon compounds, and if so whether this is driven by differences in snow pack or through concomitant vegetation changes remains unknown.

Here we test whether differences in winter snow regimes lead to carry-over effects into summer in an oceanic alpine moss heath. We also separated the direct, short-term effects of snow regime on microbial ability to catabolize carbon compounds from the longer-term effects mediated by snow-induced changes in vegetation composition, using a reciprocal transplant experiment. We hypothesized that contrasting winter snow conditions would select for different microbial communities with different functional capacities (*sensu* Zak et al., 1994) to catabolize carbon compounds during summer, but that these effects would mainly be driven indirectly by concomitant changes in vegetation composition.

On a Scottish mountain plateau (see Supplementary Information online) characterized by shallow, intermittent winter snow regime with strongly fluctuating soil temperatures and freeze-thaw events, a snow fence was erected in 1986. This caused a snow drift, below which soil temperature stayed around 0 °C during winter (Wipf et al., 2015). In response, the vegetation dominated by the moss *Racomitrium lanuginosum* and sedge *Carex bigelowii* changed to dominance by the moss *Dicranum fuscescens* and several grass species in the immediate vicinity of the fence (Scott et al., 2007; Welch and Scott, 2000; Figs. S1 and S2).

We set up a reciprocal transplant experiment in October 2006 (Wipf et al., 2015). Monoliths were dug out near (deep-snow area) and away (shallow-snow area) from the fence and were either placed back in the same place (i.e. continued exposure to local snow regime; to determine long-term impacts) or transplanted between shallow- and deep-snow

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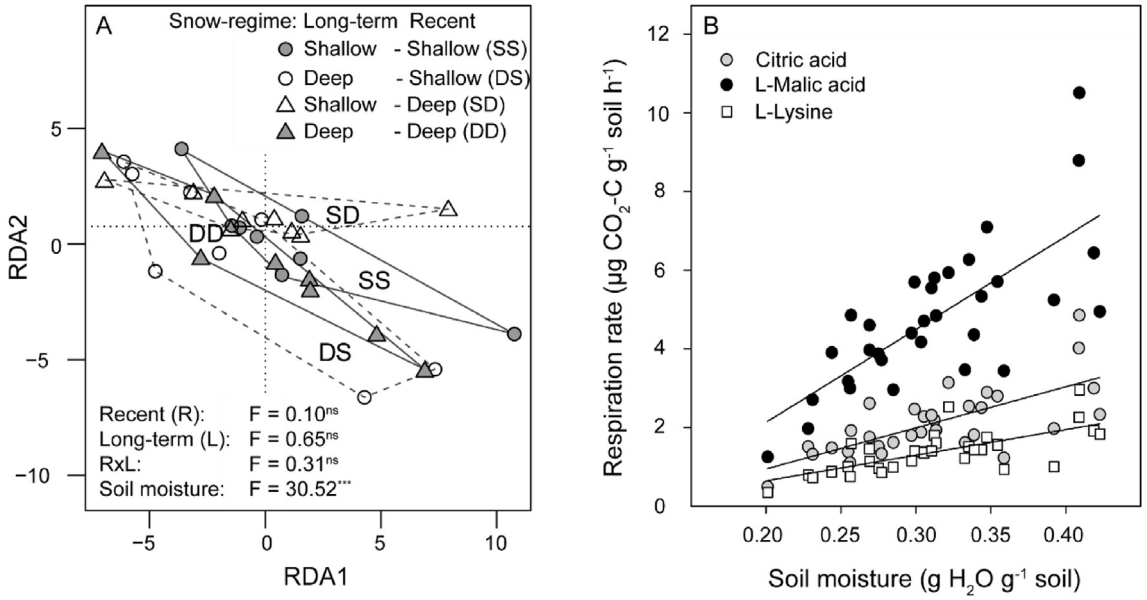

Fig. 1. A). First two constrained axes of the partial redundancy analysis on substrate-induced respiration rates. Recent (2006–2009) and long-term (1986–2006) snow regime (shallow and intermittent vs. deep and persistent) were used as predictors, after statistically controlling for the effects of sampling block and soil moisture content (conditioning matrix). The ordination spaces of measurements on soils from monoliths that remained in their original snow environment is indicated with solid lines, and those associated with monoliths that were placed in the other snow environment with a dashed line. Results of multivariate permutation tests are shown in the panel. For further details see Fig. S3. B). Soil respiration rates in response to gravimetric soil moisture content for three selected carbon sources in the MicroResp analysis (c.f. Table 1).

areas (to isolate snow effects from vegetation effects). Three years after transplanting the monoliths, the vegetation had not changed in response to the new snow regimes (Supplementary Results). Soil cores were taken in all monoliths and analysed using MicroResp™ (Supplementary Methods); a substrate-induced respiration method designed to estimate the soil microbial community's capacity to process a range of carbon sources.

Despite 23 years of contrasting snow regimes and fundamentally different vegetation composition (Figs. S1 and S2), there were no differences in substrate-induced respiration by the microbial community between soils near and away from the fence (Fig. 1A; Table S1). In addition, when these communities were exposed to the respective opposite snow regime, neither community showed any change in their carbon catabolic abilities (Fig. 1A; Table S1). Rather than observing consistent differences in respiration rates among the treatments (Table 1), substrate-induced respiration rates among the 15 investigated carbon sources were all strongly and positively correlated with soil moisture content (range 0.20–0.42 g H_2O g^{-1} dry soil, r: 0.60–0.79, n = 32, $p < 0.0005$; Fig. 1B). Likewise, multivariate analysis confirmed a strong effect of soil moisture on respiration rates (Permutation-F = 30.52, p = 0.002, $R^2 = 0.52$), but treatment effects were not visible after accounting for variation in soil moisture in the analysis (Fig. 1B, Fig. S3).

The lack of treatment differences in microbial functional capacity to process carbon compounds was surprising, given that long-term differences in snow cover led to strongly contrasting vegetation types on site, which are known to influence microbial community composition (Zinger et al., 2009). The lack of treatment differences could have been caused by soil handling disturbances, but we do not think this is the case (see Supplementary Methods for discussion). Alternatively, it is possible that the snow regimes led to taxonomically different communities without causing a measurable difference in carbon catabolism. Alpine microbial communities show rapid shifts in community composition from winter into summer (Monson et al., 2006; Schadt et al., 2003). We sampled 1.5 months after snowmelt and the seasonal turnover may already have been completed, resulting in functionally similar summer microbial communities. A meta-analysis found that snow cover drives growing season soil CO_2-efflux, but that efflux in deep snow areas is driven by higher soil moisture (Blankinship and Hart, 2012). Our findings point in the same direction: it is the soil moisture content at the time of sampling, rather than legacy effects of winter snow conditions or vegetation differences, that drives the microbial community to catabolize carbon compounds. Importantly, however, climate change not only leads to altered snow regimes, but also temperatures and evapotranspiration, and future studies are needed to investigate the combined impact of these interacting drivers.

While the snow regime governs alpine ecosystem processes during winter (Fisk et al., 1998; Wipf and Rixen, 2010), reported seasonal carry-over effects are mixed. For instance, in northern hardwood forests deeper snow caused higher growing season potential nitrifying activity and microbial respiration (Durán et al., 2014). Yet, in the same ecosystem, snow-induced changes in microbial and exo-enzyme activity did not persist into summer (Sørensen et al., 2016). Similarly, in a Canadian old-field, snow removal did not influence soil N losses during the growing season (Vankoughnett and Henry, 2013). It has been hypothesized that C and N processes may differ in seasonal carry-over effects (Durán et al., 2014), but clearly more studies are needed to disentangle the controls over microbial community functioning in the face of changing snow regimes.

We conclude that the soil moisture effect on summer microbial carbon catabolism overwhelmed the possible legacy effects associated with strong and long-term differences in winter snow cover and vegetation composition in this oceanic mountain heath. Modest differences in soil moisture content rendered any pre-existing differences in the microbial community's ability to catabolize carbon compounds insignificant, despite decades of differential snow cover and large differences in vegetation composition. Our results point to the need for future research to focus more strongly on soil moisture and hydrology effects, coupling the spatio-temporal dynamics of soil-water-atmosphere carbon cycling in the uplands.

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Table 1
Mean (± SD) microbial community respiration in response to the addition of different carbon-substrates in soil samples from under moss communities with contrasting snow regimes in the recent (2006–2009) and long-term (1986–2006) past and their combinations. A: amino-acid, C: carbohydrate, CA: carboxylic acid. Respiration rates and soil moisture content were analysed using linear mixed models, with block as random effect. Significant effects are highlighted in bold. Each factor had d.f. = 1,20, except for the analysis with soil moisture as the dependent variable (d.f. = 1,21). The set of fifteen carbon sources reflect the spectrum of carbon compounds that are commonly found in the rhizosphere and differ in their degradability (Campbell et al., 2003).

Long-term:	Shallow	Deep	Deep	Shallow	ANOVA table			
Recent:	Shallow and intermittent snow		Deep and persistent snow		Factors			
Treatment code:	SS	DS	DD	SD	Soil moisture	Recent	Long-term	RxL
Substrate	μg CO_2-C respired g^{-1} soil h^{-1}				F-values			
L-Alanine (A)	1.92 (0.69)	1.83 (0.86)	1.78 (0.63)	1.77 (0.63)	**34.72*****	0.29	0.08	0.16
α-keto glutaric acid (CA)	3.02 (0.91)	2.76 (1.76)	2.92 (0.99)	2.96 (1.43)	**39.52*****	0.04	0.01	0.23
L-(+)-Arabinose (C)	2.25 (0.72)	2.08 (1.24)	2.16 (0.72)	2.20 (1.15)	**34.63*****	0.01	0.01	0.14
L-Arginine (A)	2.43 (0.63)	2.22 (1.50)	2.57 (0.71)	2.35 (0.73)	**22.48*****	0.33	0.21	0.90
L-Cysteine-HCl (A)	2.07 (0.70)	2.09 (1.10)	2.01 (0.60)	2.01 (0.80)	**46.83*****	0.13	0.45	0.01
Citric acid (CA)	2.22 (0.65)	1.98 (1.27)	2.09 (0.62)	2.18 (0.92)	**21.82*****	0.04	0.06	0.22
D-(−)-Fructose (C)	3.59 (1.01)	3.26 (1.94)	3.48 (1.15)	3.49 (1.75)	**35.41*****	0.04	0.01	0.31
D-(+)-Galactose (C)	2.12 (0.78)	1.53 (0.96)	1.84 (0.93)	2.04 (1.25)	**27.97*****	0.24	1.23	0.79
D-(+)-Glucose (C)	3.86 (1.16)	3.51 (2.07)	3.51 (1.10)	3.77 (1.80)	**45.95*****	0.01	0.08	0.06
γ-Amino butyric acid (CA)	1.87 (0.82)	2.03 (1.33)	2.05 (0.87)	1.95 (0.84)	**25.97*****	0.06	0.99	0.01
L-Lysine (A)	1.41 (0.42)	1.33 (0.78)	1.40 (0.53)	1.36 (0.50)	**25.03*****	0.01	0.08	0.23
L-Malic acid (CA)	5.17 (1.27)	4.53 (2.80)	4.73 (1.31)	4.65 (1.91)	**36.70*****	0.11	0.01	0.82
N-Acetyl glucosamine (C)	2.05 (0.73)	1.67 (0.94)	1.81 (0.70)	2.25 (1.53)	**16.33*****	0.37	1.07	0.01
Oxalic acid (CA)	2.12 (0.73)	2.07 (1.17)	2.01 (0.93)	2.16 (0.76)	**36.68*****	0.01	0.01	0.02
D-(+)-Trehalose (C)	3.36 (1.08)	2.81 (1.49)	2.97 (0.81)	3.25 (1.54)	**37.51*****	0.01	0.77	0.33
Control (dH_2O only)	0.80 (0.28)	0.73 (0.47)	0.78 (0.23)	0.82 (0.19)	**26.60*****	0.23	0.08	0.05
Sample soil characteristics								
Soil moisture (g H_2O g^{-1} soil)	0.32 (0.06)	0.31 (0.08)	0.31 (0.04)	0.32 (0.07)	–	0.01	0.24	0.01

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.05.034.

Author contributions

SW, MS and RvdW designed the field experiment; ERJW, SJW, RvdW and MIS designed the sampling and laboratory analyses; ERJW collected the data and performed the data analysis. ERJW wrote the manuscript and all authors contributed substantially to the final version.

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